

The evolution of coloniality: the emergence of new perspectives

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Colonial breeding (that is, breeding among densely distributed territories that contain no resource other than nest sites) is an unexplained form of social reproduction that occurs in many vertebrates such as reptiles¹ (including dinosaurs)², marine mammals³, and especially seabirds, in which more than 95% of species nest colonially^{4,5}. Coloniality is an evolutionary puzzle because individuals apparently pay fitness costs to breed in high densities. Identified costs are increased transmission of parasites and diseases^{6,7}, cuckoldry⁸, increased intraspecific competition for food and mates⁶, cannibalism and infanticide¹⁶. Despite such costs, however, phylogenetic analyses show that in birds coloniality is likely to have evolved at least 20 times independently⁹. This implies that individuals must benefit from breeding near conspecifics, and that these benefits must at least balance the costs. Many hypotheses have been proposed to explain how colonial breeding may benefit the individual, but there is still little support for most of them and none appears compelling^{4,9}.

Until the end of the 1980s, most discussions of how coloniality evolved were dominated by the two hypothetical advantages of enhanced food-finding¹⁰ (review in Ref. 11) and reduced predation^{12,13}. By the end of that period, reviews concluded that avian coloniality is not a simple or unitary phenomenon and that not all breeding colonies are adaptive for the same reason⁴. Recently, however, new hypotheses involving habitat selection^{14,15} and sexual selection^{16,17} set the stage for a general framework in the study of coloniality.

The economic framework

Spatial benefits of coloniality

One of the oldest assumptions is that coloniality results from a limited number of favourable breeding sites relative to vast available foraging areas¹⁸. For instance, in elephant seals (*Mirounga leonina*), the availability of long portions of suitable coastline apparently lead to a decrease in female breeding density¹⁹. However, even if food is not limiting, this cannot explain why nesting territories should be clumped while obvious favourable neighbouring areas remain empty, as has been observed in many species^{4,6,7,14,20}. Alternatively, breeders may concentrate at the place that minimizes the mean distance travelled between the nest and foraging locations. However, Brown *et al.*²⁰ noted that because the critical assumptions of that 'geometrical model' probably seldom hold for natural populations, the model is unlikely to

The evolution of group living remains an outstanding question in evolutionary ecology. Among the most striking forms of group living are the enormous assemblages of breeders that occur in many colonial marine birds and mammals, with some colonies containing more than a million individuals breeding in close contact. Coloniality is an evolutionary puzzle because individuals pay fitness costs to breed in high densities. Despite numerous potential benefits proposed to overcome these costs, we still lack a general framework to explain coloniality. Several new hypotheses involving breeding habitat and mate selection create promising approaches for studying this enigma.

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explain the evolution of coloniality in general.

Coloniality and predation

Avoidance of predators through dilution effects or social mobbing has long been suggested as a major force in the evolution of group living and coloniality in particular^{2,7,21}. Group members, for example, can spend less time being vigilant, thereby allocating more time to other activities. This was shown by Terhune and Brillant², who found in harbour seals (*Phoca vitulina*) that the time individuals spent scanning for predators decreased with colony size. However, colonies are conspicuous and may also attract more predators, which would seriously reduce the benefits of high-density breeding⁴. Clode¹³ claimed that the greater tendency of seabirds to breed in colonies clearly suggests that aggregation, far from being a defence against predators, actually makes them more vulnerable. Overall, some studies show a negative relationship between per capita nest predation risk and nearest neighbour distance or colony size, while others have found no relationship or the opposite trend^{8,12}. The result is that the influence of predation on breeding dispersion is far from clear¹².

Enhanced food finding as a benefit of coloniality

Group living has been suggested to enhance foraging efficiency. It has been proposed that colonies or communal roosts might be 'information centres' for food finding^{22,23} (review in Ref. 11). Ever since Ward and Zahavi proposed the information centre hypothesis almost a quarter of a century ago, it has generated a series of controversies that continue today^{6,11,23}, most of which have been seriously criticized^{11,24}. To date, the finding of Charles Brown on the cliff swallow (*Hirundo pyrrhonota*) is considered to provide the most convincing evidence²². In a recent review of the evidence for the information centre hypothesis, Richner and Heeb¹¹ underlined the numerous flaws of that hypothesis, and showed that the main difficulty in testing it is that most of its predictions can alternatively be explained by local enhancement, in which the recruitment of new feeding partners occurs at the food patch rather than at the colony. Therefore, the information centre hypothesis of coloniality is often unfalsifiable^{11,24}.

The recruitment centre hypothesis

Recently, Richner and Heeb^{11,25} proposed an interesting new idea relating food-finding to coloniality. They suggested

that the benefits derived from group foraging, rather than from information transfer at the breeding colony, are more likely to favour a colony-based foraging system than the mechanism of the information centre hypothesis. The benefits derived from group foraging may outweigh the costs of revealing information on food location and could therefore explain why successful foragers return to a communal place²⁵. Richner and Heeb show, with a cost/benefit analysis, how the recruitment centre hypothesis can explain why successful foragers should return to the colony and give information once a food patch has been discovered. In agreement with earlier hypotheses involving foraging behaviour¹⁴, they conclude that high ephemerality of relatively rich food sources will reduce the effect of food competition because the duration of a food source is not strongly correlated with the rate of exploitation. Under such conditions, searching individuals may be widely dispersed, making it likely that recruitment at the colony is more efficient than waiting at the food patch for other birds to join, or recruiting them locally. The hypothesis proposes that successful foragers could benefit by using a communal site for recruiting conspecifics to their newly discovered food patch; less successful foragers could benefit by gaining information concerning food discoveries and then following the most promising individuals.

The recruitment centre hypothesis also explains why some flock leaders should give aerial displays at the colony and others may not. In fact, the existence of such displays strongly supports the recruitment centre hypothesis. Because the optimal group size and the net potential benefit in the different food patches may vary, it will pay to advertise food patch quality once back at the colony. The intensity of the recruitment signal by successful foragers should vary according to the net benefit they can derive by increasing feeding group size, giving the followers the opportunity to compare the different conspecifics that have discovered a food source²⁵. This is a situation akin to the language of bees, in which the intensity of the recruitment signal is modulated according to the overall potential benefit of the discovered food patch.

Two testable assumptions and predictions of the recruitment centre hypothesis are that, when offered experimental ephemeral food patches mimicking natural situations, (1) the net benefit of a forager at the food patch is lower at the initial discovery than after returning and feeding with the recruits, and (2) birds should stop recruiting other birds to the colony when no additional benefit can be achieved by a further increase of feeding group size²⁵. The recruiting signals⁷ at the colony are expected to be initially strong and then cease at subsequent returns²⁵. Several such experiments showed the recruiting function of food calls in some colonial species⁷. The assumptions of the recruitment centre hypothesis (i.e. high patchiness and ephemerality) can also be tested in the wild. This would lead to a more precise understanding of the fascinating link between food finding and social aggregation.

The problem of the common currency

The aforementioned hypotheses of coloniality have their basis in classical economics and share a common difficulty: the costs and benefits of coloniality are usually expressed in different currencies^{13,14,26}, and their balance is extremely difficult to assess^{4,5,8,14}. Some authors have proposed that either food finding¹³ or safety from predators¹² can by itself explain coloniality. Alternatively, it has been argued that a single benefit is unlikely to explain such a complex and widespread phenomenon⁷. Coloniality is probably the result of

multiple interacting factors^{6,9}, the balance of which may vary according to the species, population and individual¹⁷. In its classical form, the cost and benefit approach to coloniality involves a series of non-exclusive hypotheses that propose assumptions and predictions, the tests of which have yielded controversial findings. The result is that, despite more than two decades of research, we still lack a general framework to organize all the potential routes to coloniality²².

Breeding habitat selection – a new framework

Recent hypotheses stem from the observation that breeding animal distribution is the result of individual choices of a breeding site^{6,11,27}, and several authors have independently analysed animal aggregation in the framework of habitat selection (Box 1). In selecting a breeding site, individuals may rely on cues that indicate the relative quality of available patches of habitat⁹. They may have first evolved an inbred image of the physical and biological characteristics (e.g. substrate quality climate or food) of favourable habitats. Second, cues may consist of parameters that integrate multiple environmental factors, such as the presence of conspecifics^{7,11}, or specific fitness components of conspecifics, such as their reproductive success (RS)^{14,15}. Animals may also be primarily influenced in selecting a breeding patch by the characteristics of potential partners. The new hypotheses of coloniality involve the three kinds of conspecific cues that may influence an animal's decision to leave or settle in a given patch: the presence of conspecifics, the reproductive success of conspecifics, and characteristics of potential partners. The hypotheses enable tentative predictions on their potential aggregative effect (Table 1).

A definition of spatial aggregation

The observed clumping of nesting territories may involve two levels of aggregation. First, nest clumping may simply reflect local variations in environmental quality, in which case a linear relationship between local quality and local density is expected. Thus, aggregation is simply 'habitat-mediated'. There may also be additive clumping, with densities being lower or higher than expected because of variation in intrinsic local quality. We call this 'additive or real aggregation'. Some patches may be overcrowded while others that are equally favourable may be underexploited, so that there is no actual limitation in favourable nesting sites, as has been shown in various colonial birds^{16,27,14,28}. Additive aggregation would scatter the points around the expected line linking local population size to local quality when aggregation is simply habitat mediated.

The ideal free distribution

The hypotheses of coloniality involving conspecific-based habitat selection all involve some kind of ideal free distribution. This is the distribution that is expected when animals space themselves among the habitat patches in direct relation to their intrinsic quality. That distribution directly (linearly) reflects the variations in patch quality. If the environment is not patchy, animals are predicted to spread evenly throughout the habitat. In patchy environments, there is no additive aggregation (Table 1). Average of fitness over a given period of time at equilibrium is similar in different patches, but because the ideal free distribution hypothesis does not provide a behavioural mechanism by which animals can actually sample their environment, it is difficult to know how animals may track environmental variation (Table 1). Such animals would not be classified as

Table 1. Predicted nesting territory aggregation in the two frameworks proposed to explain the evolution of coloniality

Framework or hypothesis	Cues and sampling date within a breeding season	Predicted effect on animal distributions if environment is			Refs
		Homogeneous	Patchy + stable	Patchy + varying in time (but still predictable)	
Cost/benefit	Not accounted for	Difficult to make predictions because, by trying to estimate the balance of costs and benefits at population scale, the economic approach does not involve any habitat selection process			4.6.9, 12.21, 22.25
Ideal Free Distribution	A priori knowledge of patch actual intrinsic quality	Even distribution	Habitat mediated aggregation only (i.e. directly reflecting patchiness)	Habitat mediated aggregation only. No mechanism by which individuals can track habitat variability	
At equilibrium, when measured over a certain period of time, average fitness is similar in different patches					
Traditional aggregation hypothesis	Sampling of the presence (i.e. group size) or cues of forms; presence (i.e. old nests) of conspecifics early in a season	Additive aggregation expected: animals may cluster in some traditionally occupied sites	Additive aggregation expected: some favourable patches may remain empty because of tradition	Counter selected: animals may keep on going in former good patches that have deteriorated	5.7, 14.27
No clear prediction on fitness at equilibrium					
Conspecific RS hypothesis	Late sampling of reproductive success of conspecifics (i.e. public information for next breeding attempt)	Additive aggregation expected. Density dependence may generate temporary variations in local RS	Additive aggregation expected	Additive aggregation expected: animals track habitat variability	15, 29-33, 42
At equilibrium, when measured over a certain period of time, average fitness is similar in different patches					
Sexual selection (huddle-lek) hypothesis	Early sampling of secondary sexual characters of potential partners	Additive aggregation expected: animals would cluster around top males, or groups of males	Additive aggregation expected: animals cluster around top males (or groups of males) which are likely to be in best patches	Additive aggregation expected: animals cluster around top males (or groups of males) which are likely to be in currently best patches	6.16, 17.18, 36-38
No clear prediction on fitness at equilibrium					

colonial, except if the differences in quality of the various patches of habitat are very strong.

The traditional aggregation hypothesis

The first use of the ideal free distribution approach in the study of coloniality has been called the traditional aggregation (or TAG) hypothesis¹⁴, which proposes that individuals use the presence of conspecifics^{5,7}, rather than the intrinsic physical quality of the patch, to sample and select a breeding patch. The presence of conspecifics is likely to reveal the suitability of a patch¹⁴. The TAG hypothesis is thus a mixture of the ideal free distribution and conspecific attraction. The aggregating role of conspecific attraction has been demonstrated from field and laboratory experiments in many groups of vertebrates and marine invertebrates (Box 1)¹⁶. The TAG hypothesis seems to generate interesting predictions on animal aggregation. However, the use of the presence of conspecifics is probably not favoured in a rapidly changing environment. This is because there may be a time lag during which individuals continue settling in habitat that was recently of high quality but that has begun to deteriorate (Table 1).

The reproductive success-based hypothesis of colony formation

Another development of the ideal free distribution principle resulted from the suggestion that animals may use specific fitness components as cues to select habitat. Adult breeders have been shown to use their own breeding experience in deciding whether to leave a breeding patch, and

individual breeding success is known to influence nest site fidelity²⁶. Individuals also use fitness components such as the reproductive success (RS) of conspecifics to assess patch quality^{15,29,30}. In the common goldeneye (*Bucephala clangula*), for instance, Zicus and Hennes²⁹ showed that adults prospect more in nest boxes that had contained successful nests during the current season than in those in which nests were abandoned, destroyed or unused. Additionally, active cavities from which young fledge in one year are preferentially used the following year, even after discounting cavity-faithful individuals. In the spotted sandpiper (*Actitis macularia*), Reed and Oring³¹ showed that the percentage of prospectors that recruit in the following year was positively associated with the number of eggs laid during the year of prospecting. In the kittiwake (*Rissa tridactyla*), 93% of recruits were seen visiting their future colony in the year preceding first breeding, of which 79.6% were seen squatting on active nests during the absence of breeders^{32,33}. Those that squatted on active nests were the most likely to recruit in the following season³³. The use of fitness components of conspecifics predicts additive aggregation even in patchy and variable environments (Table 1).

The sexual selection hypothesis of colony formation

Whereas naturally selected advantages such as food-finding and reduced predation have traditionally been stressed as explanations for coloniality, sexual selection has been largely neglected. Sexual selection has long been assumed to operate only weakly in colonial birds, because nearly all species are monogamous, presumably resulting in

low variance in male mating success. Nevertheless, it was suggested that competition for breeding partner can produce sexual selection that may promote coloniality. Numerous recent studies have revealed that males in many socially monogamous species pursue a mixed mating strategy of pairing with one female while copulating with others³⁴. Morton *et al.*³⁵ proposed a link between extra-pair copulation and colony formation in purple martins (*Progne subis*). In that system, older males appear to benefit from high density nesting by their ability to obtain extra-pair fertilizations from the mates of younger males. However, monogamous female birds may also benefit from extra-pair copulations³⁶, and in purple martins, females were subsequently found to pursue a mixed mating strategy³⁶. When females pursue multiple matings, the same mechanisms that produce lekks are predicted to operate, resulting in the aggregation of male-defended nesting territories^{17,37}. Intriguing evidence for this idea has been found in the bearded tit (*Panurus biarmicus*) by Hoi and Hoi-Leitner³⁸. They discovered that females in colonies incite males to pursue them for extra-pair matings. Females in colonies were significantly superior in body condition than solitary females, suggesting that they were able to pay the energetic costs of intersexual chases. No differences were found in predation or foraging success between colonial and non-colonial nests. The authors conclude that high density nesting in bearded tits is produced by female mating strategies. The sexual selection hypothesis also predicts additive aggregation in every kind of environment (Table 1).

'Commodity selection' as a solution to the economic approach

Our recurrent failure in solving the puzzle of the evolution of coloniality underlines the need to develop a new framework. In fact, by only focusing on the ultimate causes of coloniality, the economic approach neglects proximate mechanisms of breeding habitat selection, and thus cannot be used to predict trends in spatial distribution of nests (Table 1). The hypotheses that incorporate conspecific cueing into habitat selection allow us to make such predictions and may provide such a new framework (Table 1). Their common assumption is that, because the economic principle is logical but impracticable, the solution may be to measure parameters—such as conspecific cues—that naturally combine the effects of all the potential costs and benefits of coloniality. The appraisal of conspecific cues is parsimonious because it does not require animals to possess complex cognitive

Box 1. Conspecific-based habitat selection and animal aggregations

The selection of habitat based on conspecific cues has long been recognized as a general mechanism of aggregation in various taxa^{17,37,39}. In many marine invertebrates, for instance, evidence that conspecific-based habitat selection generates aggregation comes from various unrelated taxa such as ascidians, coelenterates, polychaetes, polychaetes, gastropods, bivalve mollusks and crustaceans^{37,40}. In these animals, gregarious larvae use chemicals released in the environment by conspecifics to select their habitat, and settle close to established conspecifics. When given the choice between two identical substrata previously soaked with extracts of adults of their own species or of a closely related species, larvae aggregated on the substratum soaked with extracts of their own species⁴¹.

Similar evidence exists in vertebrates. Stamps⁴² used experiments to show that juveniles of a territorial lizard (*Anolis aeneus*) are attracted to previous settlers and form territorial aggregations even in the absence of patchy resource distribution. Sandwich terns (*Sterna sandwichensis*) are attracted to groups of decoys of brooding individuals⁴³, and first settle between the decoys, and then around the newly formed colony. Boulenger *et al.*⁴⁴ found in the kittiwake (*Rissa tridactyla*) that prospecting mainly occurs towards the end of a breeding season, a period when local RS can be assessed accurately in a single visit. Social attraction is often exploited in reintroduction programs in order to draw groups of released individuals to the target area. Population managers use decoys (e.g. in the Atlantic puffin *Fratercula arctica*⁴⁵), painted mimicking droppings in the griffon vulture *Gyps fulvus*⁴⁶), mounts of mud mimicking recent nests (in the flamingos *Phoenicopterus ruber*⁴⁷), and tape lures of active birds (in Leach's storm petrel *Oceanodroma leucorhoa*⁴⁸).

Further evidence of a link between aggregation and conspecific-based habitat selection mechanisms comes from the study of optimal group size. Theoretical treatments have shown that individual selection can lead to observed group sizes significantly higher than the optimal group size⁴⁹. Indeed, in highly spatially heterogeneous environments, recruitment into a good patch may occur even if it entails a net fitness cost for established breeders. Owing to the strong differences between poor and good patches, newcomers would achieve higher fitness than in the poor empty patches. Hence, because of individual selection, groups may form even when the highest fitness in some good patches is achieved by solitary individuals. This suggests that higher than optimal densities may occur in some good patches, and clusters may form even when density is negatively associated with fitness, thus paving the way to coloniality.

Such issues could be analysed by modelling the effect of various habitat selection strategies on animal spatial distribution according to environmental patchiness and variability. Forbes and Kasser⁵⁰, for instance, using a model incorporating environmental patchiness, showed that by settling at an established site, individuals gain evidence that local conditions are favourable for breeding. In territorial species, simulations by Stamps and Krishna⁵¹ showed that potential settlers always acquire larger territories when settling next to neighbours than when settling at random or when settling, at some distance from previous arrivals. This was true even when there was a strong prior-residence advantage⁵², which suggests a spatial advantage in using the presence of conspecifics in settling decisions.

Complementary theoretical support for the link between conspecific attraction and aggregation comes from the study of optimal foraging. Valone⁵³ showed that the use of public information (i.e. information on current fitness components of conspecifics) can substantially increase the foraging performance of group foragers, thus favouring socially feeding individuals. The use of foraging success of conspecifics, for instance, has been demonstrated experimentally in the starling (*Sturnus vulgaris*), and its evolutionary properties⁵⁴, as well as its implications for group foraging^{55,56} have been investigated theoretically. Valone⁵³ thus suggested that we view animals, as Bayesian prospectors that incorporate past information in their decision making. Clark and Margel⁵⁷ showed that, when birds search independently for patches of food while simultaneously observing each other, an individual always does better by joining an existing feeding flock than by feeding alone. They also showed that flocking of foraging birds, even in the absence of predators, is an equilibrium strategy (i.e. an Evolutionarily Stable Strategy)⁵⁸. Placing these results into the framework of breeding habitat selection provides theoretical arguments favouring a role for social attraction in the evolution of coloniality.

abilities to assess the numerous environmental factors that act upon fitness. Rather, animals may evaluate a suite of ecological factors using the distribution of successful conspecifics and potential mates as their sole reference. In this approach, ultimate causes and proximate cues of habitat selection are combined: the RS of conspecifics for instance is the proximate cue that allows individuals to optimize their own (ultimate) RS.

The sexual selection hypothesis of coloniality exists in the same general framework of conspecific-based habitat selection because potential partners are among the various commodities of variable quality that an individual assesses when selecting a breeding patch. The sexual selection hypothesis addresses information that is not implied in such fitness components as reproductive success. In this hypothesis, it is the heterogeneity of potential partners and mechanisms of mate choice that tends to aggregate individuals around those of higher quality. In the habitat selection hypotheses, it is the spatial heterogeneity of the environment and the use of conspecific cues that generates the aggregation of individuals. Together, the habitat and sexual selection hypotheses of coloniality involve the assessment and selection of all the commodities necessary to breed—food, safety, health, mates, fertilization, breeding sites. Thus, commodity selection may be the common thread of coloniality.

Our growing understanding that conspecific cueing can generate animal aggregation (Box 1) opens new perspectives for studying coloniality. Observing how animals use

conspecifics to select breeding habitat may allow us to predict patterns of aggregation in different environments (Table 1). This approach may circumvent the problem of balancing costs and benefits with different currencies. These costs and benefits directly affect fitness components (such as reproductive success) and potential partner quality. Using the presence or RS of conspecifics and potential partner quality as the common currency for patch choice is an indirect but efficient way to weigh costs and benefits.

The use of RS as a common currency has in fact been implicit in several cost/benefit studies of coloniality (review in Ref. 7). For example, Brown and Brown^{7,22} used chick body mass and survivorship to weigh the cost of ectoparasitism against the benefits of enhanced food finding. The RS-based hypothesis suggests that we use RS as the long-sought common currency to assess the pros and the cons of coloniality. The RS is a strong correlate of fitness; its measure implies the use of an evolutionary paradigm, which *per se* is the economic approach. In a sense the commodity selection hypothesis provides a solution to the economic approach. It encompasses all the previous approaches: the different routes to coloniality all converge at commodity selection.

The hypotheses of the commodity selection framework do not assume a shortage of favourable breeding sites. To the contrary, they all predict additive aggregation (Table 1). The use of conspecific cue rather than the actual intrinsic local quality leads to distributions that are more clumped than those predicted by the ideal free distribution alone. Indeed, such animals would try to breed as closely as possible to conspecifics with high fitness¹⁸ in order to benefit from the same favourable environmental conditions. The aggregating effect of commodity selection, however, is likely to vary according to the cues used when selecting a breeding patch and on the type of environmental variability (Table 1). It may be particularly high if individuals use the RS of conspecifics as the currency to assess local quality. However, because they are under different selective pressures, different phenotypes may be more sensitive to various cues. Accordingly, individuals may be more or less prone to aggregate, or they may show differences in preferences. In cliff swallows, for instance, Brown and Brown⁷ observed that birds sort among colony size according to age, parasite load and body condition. They hypothesized that colony size variation reflects phenotype-based colony choice, with individuals selecting the colony size that is optimal for them. Such phenotypic variation may explain the colonization of new patches even in highly gregarious species. Similarly, selective pressures in various environments may have led some species to use a particular cue preferentially, thus making some of them more prone than others to aggregate.

Because the choice of a breeding patch strongly affects individual fitness, robust decision-making rules are expected, and the empirical^{29,31–33}, experimental^{29–31} and theoretical^{15,42} evidence that animals of different taxa use the presence and success of conspecifics as cues to habitat selection shows the widespread prevalence of such mechanisms. Thus, the effects of commodity selection on aggregation are likely to be widespread in animals.

Prospects

Several assumptions and predictions of the commodity selection hypothesis of coloniality can be tested using empirical, experimental and theoretical data. In marked natural populations, empirical tests can correlate current fitness components with local recruitment and adult fidelity to the breeding site. Temporal autocorrelation can be used to study environmental predictability between breeding seasons, a

crucial issue for conspecific-based breeding habitat selection^{13,43}. Experimental tests can involve the manipulation of the suspected cues (local RS, potential mate quality) in the wild to assess the effect on local recruitment, breeding adult site fidelity, and local dynamics. For instance, experimental manipulations of the presence of conspecifics with decoys have revealed the aggregating effect of social attraction (Box 1). Such studies should also include analyses of the evolutionary function of prospecting both by immature and adult individuals before settlement. This behavioural pattern is widespread in birds but has been ignored until recent years. This would allow us to understand the links between sampling behaviour, breeding habitat selection and animal aggregation.

The commodity selection hypothesis of coloniality bridge some traditional areas of research in evolutionary ecology (habitat and sexual selection, animal aggregation, sociality and the evolution of dispersal). It also places the question of the evolution of coloniality into the general framework of animal communication and learning, and view this particular pattern of sociality as a by-product of habitat and sexual selection. The ability of individuals to assess and select all the fitness enhancing commodities (i.e. food, potential breeding sites and partners) from cues produced by conspecifics, therefore, may play a prominent role in the evolution of coloniality, and sociality in general.

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